The Family Galeonmatidae (Bivalvia: Leptonacea) in the Eastern Atlantic

by

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Abstract. Two new species of the Galeonmatidae are described from West Africa: Galeonma coalita, unusual for the genus in having valves that may close almost completely, and Ephippodonta gregaria, the first known representative of its genus in the Atlantic. Galeonma coalita and the European species Galeonma turtoni (probably also the South African species Coleoconcha opalina) have parasitic dwarf males attached to the mantle, whereas E. gregaria is hermaphroditic. The range of Galeonma turtoni also includes West Africa.

INTRODUCTION

The Galeommatidae are a family of small marine bivalves that have attracted the attention of malacologists for their unusual characters: a trend towards expansion of the mantle over the shell and the ability to crawl about on their foot. They are represented in the Indo-Pacific by many genera and species. Only two Atlantic species resemble the European *Galeomma turtoni* Sowerby, 1825, with a large ventral gape on the shell: the American Aclistothyra atlantica McGinty, 1955, and the South African Coleoconcha opalina Barnard, 1963. More species of Galeommatidae have now been described from Florida by MIKKELSEN & BIELER (1989) who provided detailed anatomical and biological data. Other genera and species from the eastern Atlantic have been assigned to the family, but without data on the living animals and, thus, with great uncertainty.

Collecting in West Africa has yielded new localities extending the known range of *Galeomma turtoni*, and material for two new species that are described herein. Field notes were taken on these and on European specimens of *Galeomma turtoni* collected alive.

Museum abbreviations used in this paper are: ANSP, Academy of Natural Sciences, Philadelphia; MNCN, Museo Nacional de Ciencias Naturales, Madrid; MNHN, Muséum National d'Histoire Naturelle, Paris; SAM, South African Museum, Cape Town; USNM, National Museum of Natural History, Washington.

TAXONOMY

Family GALEOMMATIDAE Gray, 1840

Galeommatidae (corrected name, herein, for Galeomatidae Nordsieck, 1969, incorrect original spelling) is a junior homonym and synonym. Ephippodontidae (corrected name, herein, for Ephippiodontidae Scarlato & Starobogatov, 1979), type genus *Ephippodonta* Tate, 1889, is considered a synonym.

Genus Galeomma Turton, 1825

- Original reference: TURTON, 1825:361, pl. 13, fig. 1. Type species: Galeomma turtoni Sowerby in TURTON, 1825, by monotypy (see ICZN, Art. 69a, vii).
- Synonym: Parthenope Scacchi, 1833 (type species: P. formosa Scacchi, 1833, by monotypy).

Galeomma turtoni Sowerby in Turton, 1825

- Original reference: TURTON, 1825:361, pl. 13, fig. 1. Type material: Holotype USNM 199412 (WARÉN, 1983:pl. 9, figs. 5-8).
- Synonyms: "Hiatelle de Poli" Costa, 1828 (vernacular); Hiatella Poli Costa in Scacchi, 1836, Hiatella poliana Costa in Philippi, 1844 (both first published as a synonym and not available). Parthenope formosa SCACCH1, 1833:8-10, 19.

Galeomma pileum BRUSINA, 1866:42–43.

Material examined: European Atlantic and Mediterranean—Herm, Channel Islands, 4 shells (Staadt collection, MNHN); Roscoff, Brittany, 2 shells (*leg.* Gofas 1976, MNHN); Guethary, Basque coast, Bay of Biscay, 3 specimens (*leg.* Gofas September 1988, MNHN); Sagres, Algarve, southern Portugal, 4 specimens (Mission Algarve, May 1988, MNHN); Cabo de Gata, Spain, 1 specimen (*leg.* Hergueta March 1986, MNCN); Marseille, 5 specimens (old collection MNHN); Marseille, 3 specimens (Jousseaume collection, MNHN); Toulon, 4 specimens (Petit collection, MNHN); Giottani near Cap Corse, Corsica, 2 specimens (MNHN). New occurrences—Ouaran,



Explanation of Figures 1 to 5

Figures 1-5: Galeomma turtoni Sowerby in Turton.

Figure 1. Exterior of shell of adult female from Guethary, Bay of Biscay (actual length 8.6 mm).

Figure 2. Protoconch and initial part of teleoconch of the same specimen as in Figure 1 (scale bar is 100 μ m).

Figure 3. Shell of dwarf male attached to the same specimen as in Figure 1 (actual length 770 μ m).

Figure 4. Exterior of left valve and interior of right valve of a specimen from Cabo Ledo, Angola (actual length 5.4 mm).

Figure 5. Protoconch of specimen in Figure 4 (scale bar is 100 μ m).

near Dakar, Senegal, among rocks (*leg.* Bouchet August 1973, MNHN); Cabo Ledo, Angola, under stones taken in fishing nets 10–40 m, 2 specimens (*leg.* Gofas, MNHN).

Habitat: Inside large crevices in rocks or other hard substrata, from just below low tide level to ca. 20 m, crawling free or byssally attached, generally isolated or in small numbers.

Selected measurements (in millimeters, length \times maximum height from umbo to margin):

Guethary	8.6×4.0	Marseille	13.4 × 6.3
	7.3×3.5		9.2 × 4.9
			9.2 × 4.3
Algarve	9.6 × 4.4		8.2×4.0
-	8.8 × 4.3		8.1 × 4.3
	7.8×3.8		8.0×3.8
	6.3×2.9		
		Corsica	6.7×3.3
Herm	12.4×5.3		5.5×2.8
	10.8×5.2		
	10.6×5.1	Almeria	6.7 × 3.4
	10.3×5.1		

Remarks: The morphology and anatomy of this species have been described in detail by several authors, among them MITTRE (1847), PELSENEER (1911:44-45, pl. 16), and POPHAM (1940). BRUSINA (1866) distinguished *Galeomma pileum* as being shorter, more oval, and more markedly depressed laterally. This description is here considered to fall within the variability of *G. turtoni*.

Two specimens from Guethary, Bay of Biscay, have each been observed to host a dwarf individual attached to the ventral part of the mantle, near the edge of the valve. One of these has been sectioned (personal communication, G. Rodriguez, University of Oviedo). The large individual was a female. The small specimen has only a reduced foot and mantle, and a male gonad occupying its entire internal volume.

The shells of the other pair were photographed under SEM (Figures 1-3). The large shell is 9 mm long and has a smooth protoconch consisting of hemispherical valves 310 μ m in diameter. These are separated from the teleoconch by a sharp boundary, and the radial ribs of the teleoconch start exactly from that boundary. The smaller attached shell is 740 μ m long, with a protoconch similar in size and shape to that of the larger shell. Its teleoconch is very small, with sculpture consisting only of irregular, coarse growth lines, and no radial ribs.

A brooding specimen from Sagres, southern Portugal, was seen releasing spawn, eggs or small larvae less than 100 μ m in size, in May 1988. The morphology of the larval shell, with recognizable protoconch-1 and protoconch-2, and the abrupt protoconch-teleoconch boundary suggest that there is planktotrophic larval development.

Specimens collected in Angola (Figures 4, 5) are separated from the nearest northward locality (Ouaran, Senegal) by a large gap. The distribution of the species may be disjunct, like that of many West African bivalves (R. von Cosel, personal communication).

Galeomma coalita Gofas, sp. nov.

(Figures 6-8)

Type material: Holotype (MNHN), live-taken specimen and attached allotype: Caotinha, under stone at low tide mark, *leg.* Gofas, December 1985.

Paratypes (all leg. Gofas, 1983-1986, MNHN): An-

gola—Bango, 10 km S Ambrizete, province of Zaire, 1 valve (Figure 6); Praia São Tiago, province of Bengo, 1 valve; Barra do Dande, province of Bengo, 1 juvenile valve; São Nicolau, province of Namibe, 1 live-taken specimen (left valve crushed), under stone at low tide mark.

Type locality: Caotinha (12°36'S, 13°15'E), Benguela Province, Angola.

Other material examined: Senegal—Baie de Gorée, south of Tacoma, 25 m, 1 valve (*leg.* Marche-Marchad, MNHN); SE of Gorée, in fine muddy sand, 17 m, 1 valve (*leg.* von Cosel 24 March 1988, MNHN).

Habitat: The living specimens were found under stones, byssally attached to the rock surface.

Description: Shell 8–11 mm long, thin and fragile, equivalve, slightly inequilateral with beaks anterior to the vertical midline. Outline oval-elongate with dorsal margin straight along ca. γ_{10} of the total length, anterior and posterior margins well rounded, and ventral margin nearly straight beneath the umbos. Protoconch with hemispherical valves, 300 μ m in diameter, smooth, demarcated from the teleoconch by a distinct line. Teleoconch with a reticulate external sculpture of radial riblets and concentric threads; the interspaces 2–3 times as broad as the riblets. Radial ribs divergent along the anterior and posterior slopes of the shell. Additional riblets added in the interspaces, and a few riblets terminating without reaching the margin of the shell. Shape laterally compressed, with valves almost closing ventrally.

Hinge line smooth, interrupted under the umbo by a small resilifer, of different shape on the two valves. Left valve with a small vertical notch just beneath umbo and an oblique toothlike structure next to it posteriorly; right valve with a very oblique notch opposite to the toothlike structure of left valve, and hinge line abutting anteriorly to it with a small knob. Internal ligament short, in resilifer; external ligament thin, extending along hinge line.

Inside of valves with a broad, irregular, entire pallial line merging into the muscle scars. Scar of anterior adductor larger and closer to dorsal line than that of posterior adductor. Scar of posterior pedal retractor large, above the posterior adductor. Inner area beneath the umbo slightly granulated.

Mantle (Figure 8) thin and translucent, covering outer two-thirds of shell with tiny (ca. $200 \,\mu$ m) papillae scattered over surface. One short tentacle attached at each end of hinge line.

Dwarf individual found attached by its foot to mantle of holotype, close to middle part of ventral margin: protoconch as above, teleoconch with leaf-shaped valves, gaping ventrally, pointed anteriorly and posteriorly, and with sculpture of coarse concentric growth lines only.

Selected measurements (in millimeters, length \times maximum height from umbo to margin):



Explanation of Figure

Figures 6-8: Galeomma coalita Gofas, sp. nov.

Figure 6. Exterior of a paratype (right valve) from Bango, near Ambrizete, Angola (actual length 7.3 mm).

Figure 7. Detail of hinge and protoconch of a specimen from Bay of Gorée, Senegal (scale bar is 100 μ m).

Figure 8. Ventral view and lateral view of right side of the holotype from Caotinha, Angola (actual length 10.6 mm). Note attached dwarf male and membranous mantle covering the outer two-thirds of the shell.



Explanation of Figures 9 to 15

Figures 9-15: Ephippodonta gregaria Gofas, sp. nov.

Figure 9. Exterior of right valve and interior of left valve of the holotype from Cape Palmeirinhas, Angola (actual length 6.9 mm).

Figure 10. Detail of ornamentation of the holotype (scale bar is 100 μ m).

SE of Gorée

Barra do Dande

Caotinha (holotype)	10.6×5.5 and attached allotype
	0.9
São Nicolau	10.0×5.0
Baie de Gorée	9.2×4.5
Bango	7.3×3.6 (Figure 6)
Praia São Tiago	7.8×4.0

 6.9×3.6

 4.0×1.9

Remarks: This species differs from *Galeomma turtoni* by being more compressed laterally, by its non-gaping valves, and by the much smaller size of the mantle papillae. The dwarf specimen is presumed to be a parasitic male as in *G. turtoni*. In *G. coalita*, it is attached to the outside, not beneath the valve edge as in *G. turtoni*. The hinge line is different in *G. turtoni*, where the small oblique resilifer is symmetrical. Details of ornamentation and sexual dimorphism are very similar to those in *G. turtoni*, and I consider that the species are congeneric.

Galeomma japonica Adams, 1862, type species of the genus *Pseudogaleomma* Habe, 1964, has a closing shell like *G. coalita*. It is otherwise reported to have a "granulated" sculpture, and nothing is known about its reproduction. More has to be known about *G. japonica* to decide if *Pseudogaleomma* may be synonymized with *Galeomma*.

Genus Ephippodonta Tate, 1889

Original reference: TATE, 1889:63–64. Type species: Scintilla (?) lunata Tate, 1887, subsequent designation by MITCHELL, 1890:32.

Ephippodonta gregaria Gofas, sp. nov.

(Figures 9–18)

Type material: Holotype and 20 paratypes, all from the type locality (*leg.* Gofas and Fernandes, February 1987, MNHN); 5 paratypes, same locality (*leg.* Rolán, MNCN).

Type locality: North of Buraco inlet (09°05'S, 12°58'E), near Cape Palmeirinhas, Luanda Province, Angola.

Other material examined: Caotinha, province of Benguela, 1 juvenile specimen (*leg.* Gofas, MNHN).

Habitat: In crevices between rocks and the bases of large oysters *Striostrea denticulata* (Born, 1778), in 1–2 m depth below low tide. Specimens were found to line the cavity between the cemented oyster valves and the substratum,

aggregating in large numbers. No particular association was noted, but the cavities also hosted sponges and crustaceans.

Description: Shell 6-8 mm long, thin and fragile, equivalve, almost equilateral. Outline oval-elongate with dorsal margin straight along ca. 3/10 of the total length, anterior and posterior margins well rounded, and ventral margin broadly rounded. Protoconch with hemispherical valves, with protoconch-1 hardly distinct, smooth, ca. 100 µm in diameter, and protoconch-2 ca. 270 μ m in diameter, smooth, separated from the teleoconch by a distinct line. Teleoconch with a strongly inflated, smooth umbonal area, then rather flattened with external sculpture of tiny (20 µm) granules arranged regularly along concentric and radial lines. Granules connected along concentric lines by a fine thread; the interspaces slightly larger than the granules between concentric rows, smaller between radial lines. Radial rows of granules divergent along the anterior and posterior slopes of the shell, with additional radial lines of granules added there in the interspaces. Transverse profile with valves normally opened at ca. 180° when alive, unable to close completely because of hinge and ligament structure.

Center of hinge line with two strong toothlike thickenings symetrically developed on each valve and abutting against each other but not interlocking; the anterior one larger, the posterior one small and mucronate. Resilium strong, permanently bent to maintain the valves open, wedged in between the toothlike thickenings. Remainder of hinge with minute crenulations, irregularly spaced and not clearly alternating nor facing each other.

Inside of valves (Figure 17) with a broad, irregular, entire pallial line merging into the muscle scars. Scar of anterior adductor slightly closer to dorsal line than that of the posterior adductor. Scar of posterior pedal retractor large, above the posterior adductor.

Mantle (Figure 16) covering entire shell, equipped with large (200–500 μ m) pedunculate papillae scattered over dorsal surface, and fingerlike tentacles of comparable size forming fringe along edge of valves. One tentacle at each end of hinge line, small at rest but projecting to several times its original size when animal is immersed in formalin. Two pallial openings next to these tentacles, the posterior one smaller and closed, the anterior one connected ventrally with a large pedal gape. Ventral part of mantle smooth, with a definite groove parallel to the edge of the valves and its central part swollen. Foot elongated, capable of crawling, with a ventral longitudinal groove.

[←]

Figure 11. One of the granules, magnified (scale bar is 10 μ m).

Figure 12. Exterior of the shell of a paratype (actual length 5.0 mm).

Figure 13. Left valve of another paratype (young specimen) showing smooth umbonal area (actual length 2.5 mm).

Figure 14. Protoconch of another paratype (arrow indicates protoconch-1/protoconch-2 boundary; scale bar is 100 μ m).

Figure 15. Detail of hinge of another paratype (scale bar is 500 μ m).



Explanation of Figures 16 to 18

Figures 16-18: Ephippodonta gregaria Gofas, sp. nov.

Figure 16. Dorsal and ventral view of a living specimen from Cape Palmeirinhas, Angola (actual length, excluding foot, 7.0 mm; anterior end up).

Figure 17. Internal view of the shell of a paratype (same specimen as fig. 12) showing pallial line and muscle scars (actual length 5.0 mm).

Figure 18. Detail of gills (od, outer demibranch; id, inner demibranch), labial palps (lp), and foot (f) of a preserved specimen, mantle removed (scale bar is 1 mm).

Selected measurements (in millimeters, length \times maximum height from umbo to margin):

Cape Pal-	7.2	×	3.6		6.3	×	3.2
meirinhas:	7.2	×	3.4		6.1	х	3.1
	7.1	×	3.2		5.7	×	2.8
	6.9	×	3.9	(holotype)	4.5	×	2.7 (figured
	6.8	×	3.1				paratype

Remarks: This species closely resembles the type species of the genus, *Ephippodonta lunata* (Tate, 1887), in the shape of the valves and the type of shell ornamentation with nodules arranged radially and concentrically. Also similar is the hinge line with strong thickenings abutting against each other and with no definite teeth. The Angolan species differs in having still smaller granules ornamenting the shell. A gregarious occurrence was also noted for *E. lunata* by MATTHEWS (1893): "One occasionally finds immense numbers of minute *Ephippodonta* lining the [shrimp] burrows."

Ephippodonta murakamii Kuroda, 1945, (type species of the subgenus *Ephippodontina* Kuroda, 1945, by original designation) differs in having weakly developed but distinct teeth on its hinge line. KURODA's (1945) illustrations show a finely reticulate ornamentation of concentric threads and radial riblets; these diverge along an anterior and a posterior radial line and sometimes bifurcate, in a pattern very similar to that of *Galeomma turtoni*. ARAKAWA (1960: 57) states about *E. murakamii* that "the shells are never wrapped with the expanded mantle."

Ephippodonta (Ephippodontina) oedipus Morton, 1976, differs in having much smaller, non-pedunculate papillae on the mantle and a more Galeonma-like reticulate ornamentation on the shell.

No dwarf males have been found on the mantle of examined specimens of *Ephippodonta gregaria* sp. nov. Eight specimens were sectioned; all contained spermatozoa, and five of them also contained ovules, which indicates that the species is hermaphroditic (personal communication, G. Rodriguez, Oviedo). Five of these eight specimens contained larvae, less than 100 μ m in length and oval-elongate in shape, brooded in the gills. The full grown protoconch seen on the adult shell is much larger than those brooded larvae. There is a clear boundary (Figure 14) separating protoconchs 1 and 2, indicating a planktotrophic larval development.

The ability to extrude the two tentacles anterior and posterior to the hinge line was also reported for *Galeomma polita* (Deshayes, 1856) by MORTON (1976), and was interpreted as a defensive behavior.

I have examined one paratype (one valve, ANSP catalogue no. 194067) of Aclistothyra atlantica McGinty, 1955 (type species of Aclistothyra McGinty, 1955, by original designation). It is superficially similar to Ephippodonta gregaria, but the hinge line is not crenulated, there are no cardinal teeth nor thickenings, the resilifer is small, and the valves are more flattened, not swollen in the umbonal area. The external sculpture is not "granular" as ambiguously suggested in the original description, but minutely pitted, and the pits are arranged in an alternating pattern and not radially. The pits are larger and more irregularly arranged close to the edge of the shell, becoming smaller and more regular towards the umbo. This microsculpture is coarser than the granules of the Angolan species. The protoconch in *A. atlantica* is smooth with hemispherical valves, ca. 380 μ m in diameter, and is separated from the teleoconch by a distinct line. This is very similar to the condition in *Galeomma, Ephippodonta,* and *Coleoconcha,* and also suggests a planktotrophic larval development.

Genus Coleoconcha Barnard, 1963

Original reference: BARNARD, 1963:33. Type species: C. opalina Barnard, 1963, by monotypy.

Coleoconcha opalina Barnard, 1963

Original reference: BARNARD, 1963:33-35.

Material examined: Syntype, 1 live-taken specimen preserved in alcohol, South African Museum, Cape Town, catalogue no. SAM 29642, exposed side of Schaapen Island, Langebaan (Saldanha Bay), *leg.* R. Dick, 24 April 1962.

Remarks: The two larger specimens mentioned by BARNARD (1963:34) are at this time missing from the South African Museum (J. Pether, in litt.). The collecting data and dimensions of the specimen illustrated here (Figure 19) fit the "smallest specimen" mentioned by Barnard and identify it as a syntype.

The shell is badly damaged by acidic alcohol. The protoconch is smooth, with hemispherical valves about 500 μ m in diameter, and an abrupt protoconch-teleoconch boundary. The teleoconch shows mostly growth lines, with several marked growth stages, and a minute crenulation of the posterior edge of the valves. Similar crenulations also appear anteriorly and are repeated along growth stages, according to BARNARD's (1963) description and illustration of the largest syntype.

Coleoconcha opalina has low, broadly spaced mantle tubercles, a straight hinge line devoid of teeth, and conspicuous labial palps. It resembles *Galeonma* most closely because of these characters.

The "juveniles (protoconchs) attached symmetrically on either side of the mantle," 0.75 mm long, observed by BARNARD (1963) on the largest specimen are presumably dwarf parasitic males as in *Galeonma*.

LARVAL DEVELOPMENT AND SEXUAL STRATEGIES

The larval shell of bivalves reflects patterns of larval development in the same way as that of gastropods. That is, a visible boundary between a small protoconch-1 and a protoconch-2 is evidence for a pelagic, planktotrophic development. In accordance with this similarity, I have called



Figure 19

Coleoconcha opalina Barnard, 1963. Ventral and dorsal view of syntype (SAM 29642, actual length 3.0 mm, anterior end up).

the larval shell a "protoconch," notwithstanding the widespread use of the term "prodissoconch" in the literature on bivalves.

A sequence of brooding of larvae in the pallial cavity in an early stage and then pelagic development is inferred for *Galeomma turtoni* and *Ephippodonta gregaria*, on the grounds that larvae less than 100 μ m in diameter were seen brooded or just released, whereas the protoconch on the adult shell is nearly 300 μ m in diameter with a recognizable boundary between protoconch-1 and protoconch-2 (Figures 3, 5, 14). The release of "shell-less larvae" was also observed for *Galeomma turtoni* by POPHAM (1940).

Brooding followed by pelagic larval development is most common among the Leptonacea (LEBOUR, 1938; CHANLEY & CHANLEY, 1970; O'FOIGHIL, 1988; MIKKELSEN & BIE-LER, 1989; and references therein). A few species brood their larvae until they are released with so-called "direct" benthic development (e.g., DEROUX, 1960; OLDFIELD, 1964).

Dwarf males, attached to the outside of adult females, were seen in both Atlantic species of *Galeomma* and inferred to exist in *Coleoconcha*. The occurrence of parasitic dwarf males has been documented many times in the Leptonacea. Shelled dwarf males such as in *Galeomma* have been reported for *Ephippodonta oedipus* by MORTON (1976).

In Montacuta phascolionis Dautzenberg, 1925 (Leptonacea: Montacutidae), accessory dwarf males are brooded in the pallial cavity with the larvae and maintain many larval features; the larger host individuals, however, also develop spermatozoa (DEROUX, 1960). Dwarf males have been reported associated with larger females in "Pseudopythina" subsinuata (Lischke, 1871) (MORTON, 1972), and brooded in the pallial cavity of "Pseudopythina" rugifera (Carpenter, 1864) (O'FOIGHIL, 1985). Both species are interpreted as protandric hermaphrodites, with further development of the male outside the female shell, and sex reversal. Extreme reduction of the males is seen in Montacuta percompressa (Dall, 1899), where they are reduced to shell-less masses of gonad, 500 μ m in diameter, parasitic on the females (JENNER & MCCRARY, 1968).

In the case of *Galeomma* (Figures 2, 3), the initial part of the teleoconch differs between the "normal" shells of females and the shells of dwarf attached males. This means that sex is already determined at the time of settling and the dwarf males will not eventually grow into larger females. A likely scheme would be that sex determination is induced by the presence or absence of a female at the time of settling.

The taxonomic significance of the reproductive features is yet to be evaluated. Morphological similarity in the larval shells of planktotrophic *Galeomma*, *Aclistothyra*, *Ephippodonta*, and *Coleoconcha* are a clue to close a relationship. The family may also include, however, nonplanktotrophic species and, in this case, protoconch morphology may be different. The occurrence of dwarf males is not definitive at the family level; it has been documented in other, not closely related, small leptonacean bivalves (e.g., Montacuta). Conversely, all other characters suggest that the hermaphroditic Ephippodonta gregaria and the sexually dimorphic Galeomma should be placed in the same family. If one assumes that Ephippodonta oedipus is a true Ephippodonta and not a Galeomma, the occurrence of dwarf males is not even definitive within one genus.

A comparable array of sexual strategies is documented for the Eulimidae, a family of small gastropods parasitic on echinoderms (WARÉN, 1984). The possible advantages of sexual dimorphism for a parasite stated by WARÉN (1984:24) do not obviously apply to the case of Galeommatidae where dwarf males were seen on free-living *Galeomma*. The association of a dwarf male may well be advantageous for any species (parasite or not) where planktotrophic development ensures easy dispersal of larvae and, as with *Galeomma*, the adults are scattered, isolated individuals.

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